

EXTERNAL GENITALIC MORPHOLOGY AND COPULATORY
MECHANISM OF *CYANOTRICHA NECYRIA* (FELDER)
(DIOPTIDAE)

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ABSTRACT. External genitalia of *Cyanotricha necyria* (Felder) exhibit characters that occur in the Notodontidae and Dioptidae. These provide further evidence that the two groups are closely related. Dissection of two *C. necyria* pairs *in copulo* revealed two features unique among copulatory mechanisms described in Lepidoptera. First, only the male vesica, rather than the aedoeagus and vesica, are inserted into the female. Secondly, during copulation the female is pulled into the male abdomen, and his eighth segment applies dorsoventral pressure on the female's seventh abdominal segment. This mechanism is facilitated by a long membrane between the male eighth and ninth abdominal segments. The first trait is probably restricted to only some dioptid species, while the second may represent a synapomorphy for a larger group that would include all dioptids, and all or some notodontids.

Additional key words: Noctuoidea, Notodontidae, Josiinae, functional morphology.

Genitalic structure has been one of the most important sources of character information in Lepidoptera systematics. Taxonomists often use differences in genitalic morphology to separate species, and homologous similarities have provided characters for defining higher categories in Lepidoptera classification (Mehta 1933, Mutuura 1972, Dugdale 1974, Common 1975). Unfortunately, we know little concerning functional morphology of genitalia. A knowledge of function may aid in determining homology of genitalic structures, something that has proved to be extremely difficult and controversial. In addition, a functional approach can provide important new characters for understanding phylogenetic relations. For example, Stekolnikov and Kuznetsov (1982) used functional morphology of male genitalia to provide characters for higher classification of ennomine geometrids, and Stekolnikov (1967a) contributed new data concerning familial relations among butterflies. In this paper I describe the external genitalia and mechanism of copulation in a dioptid moth, *Cyanotricha necyria* (Felder).

Forbes (1939) was among the first to examine musculature of male genitalia in Lepidoptera, and his study provided the basis for subsequent research (Birket-Smith 1974). Several workers have described musculature of male and female butterfly genitalia (Shirozu & Yamamoto 1953, Hannemann 1954a, 1954b; Ehrlich & Davidson 1961, Stekolnikov 1967a), while there have been fewer such studies on moths (Hannemann 1957, Stekolnikov 1967b).

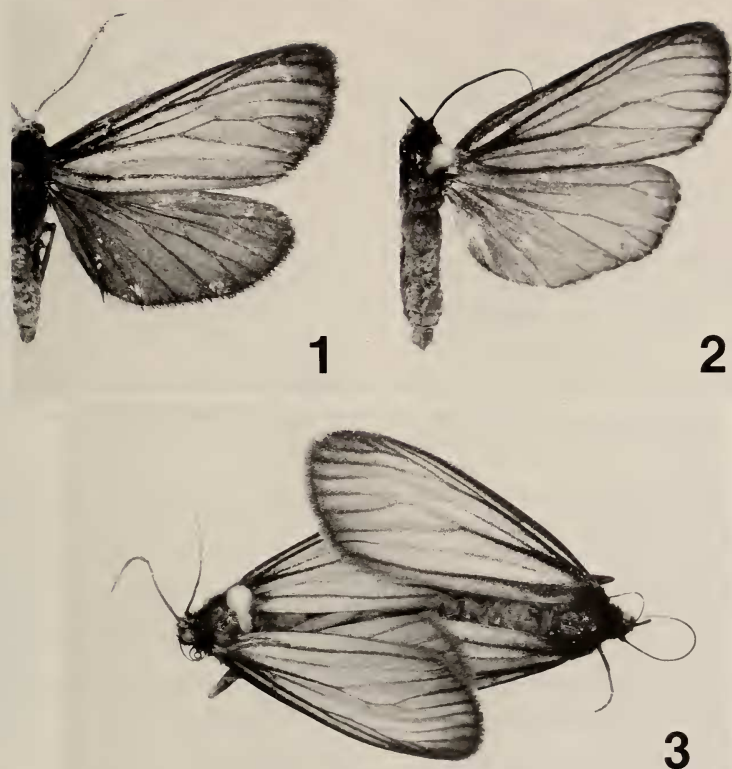
Studies of copulatory mechanisms in Lepidoptera are rare. Perhaps

the first was that of Chapman (1916a, 1916b), who attempted to determine the mechanism of copulation in lycaenids. However, he was unable to adequately preserve specimens *in copulo*. Arnold and Fischer (1977) analyzed genitalic muscle attachments and the method of copulation in three *Speyeria* species (Nymphalidae), and De Jong (1978) described the copulatory mechanism in *Carcharodus boeticus* Reverdin (Hesperiidae). Stekolnikov (1965) compared copulatory mechanisms of four moth species, *Spilosoma menthastri* Esper (Arctiidae), *Acrionicta rumicis* L. (Noctuidae), *Antheraea pernyi* Guérin (Saturniidae), and *Dendrolimus pini* L. (Lasiocampidae). In a remarkable series of papers, Callahan (1958, 1960), Callahan and Chapin (1960), and Callahan and Cascio (1963) presented a detailed analysis of copulation, spermatophore production, and egg formation in Noctuidae. They examined 11 noctuid species, including *Helicoverpa zea* (Boddie), *Pseudaletia unipuncta* (Haworth), *Peridroma saucia* (Hübner), and 8 members of Plusiinae. Their methods included serial dissection of moth pairs at various stages during copulation.

The study described here is the first on moths related to notodontids, and illustrates some unique features concerning their genitalia and mechanism of copulation. *Cyanotricha necyria* is a member of Diopitidae, a group comprising approximately 400 species of diurnal, Neotropical moths (Bryk 1930, Hering 1925). Although it is acknowledged that they are closely related to Notodontidae (Franclemont 1970), their precise phylogenetic position remains unresolved; the group may ultimately be reclassified as a notodontid tribe (Minet 1983, Miller 1987, S. Weller unpubl.). The genus *Cyanotricha* Prout, which contains only two species, *C. necyria* and *C. bellona* (Druce), was placed by Kiriakoff (1950) in the diopitid subfamily Josiinae, a well-defined monophyletic group of approximately 100 species (J. Miller unpubl.). *Cyanotricha necyria* (Figs. 1 & 2) is an iridescent blue-green moth with an orange-brown dash at the forewing base between veins Sc and Rs, and a forewing length between 15 and 18 mm. It is found from central Peru N to southern Colombia, whereas the other *Cyanotricha* species, *C. bellona*, which is less common in museum collections, has been recorded only in central Peru at elevations up to 4200 m. Like many other members of Josiinae, *C. necyria* larvae feed on *Passiflora* (Passifloraceae), and the moth is currently being tested as an agent to control the spread of *P. mollissima* (HBK) Bailey, a forest weed in Hawaii (Markin et al. in press).

METHODS

Two pairs of pinned *Cyanotricha necyria*, preserved *in copulo*, were found in the collection at the United States National Museum. Each



FIGS. 1-3. *Cyanotricha necyria* (Felder) in dorsal view. 1, Male; 2, Female; 3, *In copulo*, male at left.

had been prepared by putting a pin through the male thorax, and the wings of the male and female had been left folded (Fig. 3). According to label data, both pairs were from the Dognin collection and had been collected in the "Environs de Loja", Ecuador, by Abbé Gaujon, one pair in 1885 and the other in 1886.

For both pairs I used the same dissecting technique. The abdomens were broken from the male and female thoraces and placed, still joined, in 10% KOH for 12 h. They were then moved to 70% ethanol, cleaned of scales and soft tissues, and drawn using a camera lucida attached to a dissecting microscope. Drawings were made at two points during dissection: (1) with abdominal segments 1-6 of the male and female removed; and (2) with abdominal segments 7 and 8 and the left valve

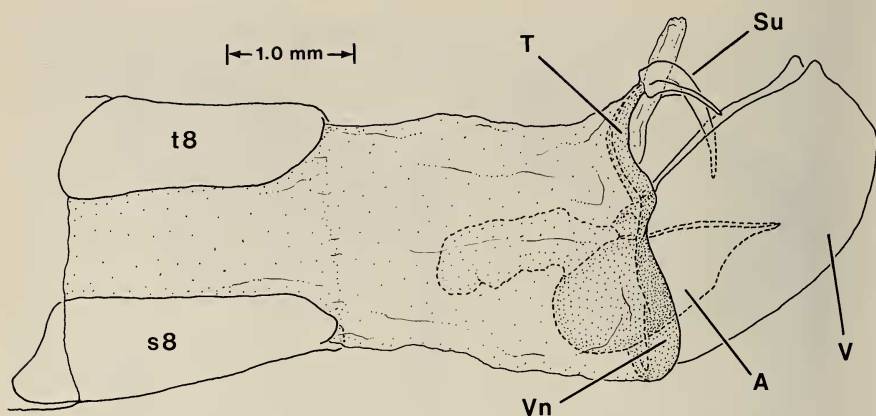


FIG. 4. Male terminalia of *C. necyria* in lateral view, anterior at left. A, aedoeagus; s8, sternite 8; Su, uncus; T, tegumen; t8, tergite 8; V, valve; Vn, vinculum.

of the male removed, and abdominal segment 7 of the female removed. These drawings were overlaid to produce Fig. 11.

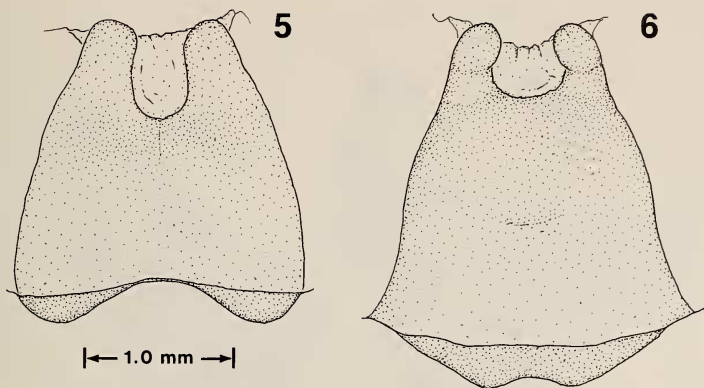
To better understand genitalic morphology in *C. necyria*, I dissected three additional males and three additional females, all from the same locality and collector as the pairs taken *in copulo*. The unpaired specimens were prepared and stained using techniques previously described (Miller 1987). All preparations are in the U.S. National Museum, Washington, D.C.

Morphological terminology follows Klots (1970), Sibatani (1972), and Ogata et al. (1957). Rather than follow the recommendation of Ogata et al. and Sibatani, who proposed the term *sociuncus*, I use two terms, *socii* and *uncus*, following Klots.

RESULTS AND DISCUSSION

General Features of *Cyanotricha necyria* Genitalia

External genitalia of *C. necyria* exhibit features unique to notodontids and dioptids. These strengthen the argument that the two groups are closely related. In *C. necyria* there is a long membrane between segment 8 and the tegumen + vinculum (Fig. 4). The latter are collectively termed the ring, which is thought to be homologous with abdominal segment 9 (Snodgrass 1935, Klots 1970). Genitalia in this species are normally enveloped within the abdomen. In *Speyeria*, where there is also extrusion of male genitalia during mating, movement is effected by protractor and retractor muscles, aided by hemolymph pressure (Arnold & Fischer 1977). An extremely long membrane between segments 8 and 9, combined with ability to withdraw genitalia inside the



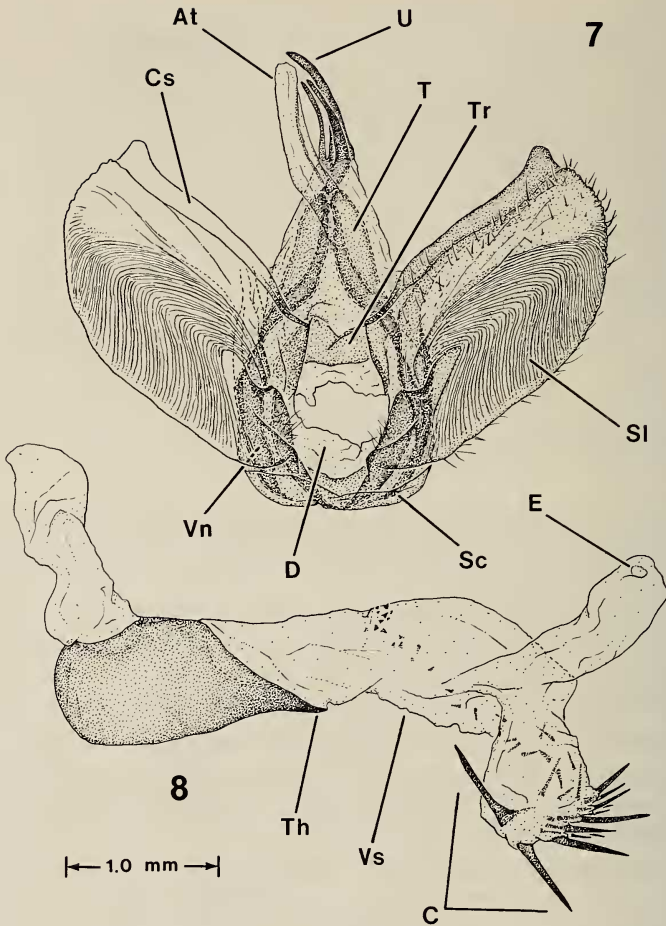
FIGS. 5, 6. Male eighth abdominal segment of *C. necyria*. 5, Tergite (dorsal view); 6, Sternite (ventral view).

abdomen, is typical of dioptids, but is also found throughout Notodontidae (Mehta 1933). This trait may represent a synapomorphy for the notodontid-related groups.

The male eighth abdominal segment in dioptids and notodontids is usually modified. In *C. necyria* there are excavations along the posterior margins of the tergite and sternite, and apodemes on their anterior margins (Figs. 5 & 6). In many dioptids and notodontids the posterior margin of the sternite and tergite is heavily sclerotized, sometimes bearing spines (J. Miller unpubl.). There is also much variation in shape of the apodemes on the anterior margin of sternite 8; they are frequently much longer than in *C. necyria*.

The sacculus of the valve in *C. necyria* is large with numerous pleats (Fig. 7), and the rest of the valve, except for the costa, is membranous. The pleated sacculus was described by Barth (1955) for *Hemiceras* (Notodontidae), but is another feature found frequently in dioptids and notodontids (Forbes 1942, Holloway 1983, Miller 1987). The pleats enclose androconia, and probably unfold during courtship, extruding the scales, which then presumably disseminate male scent. Mehta (1933) characterized notodontids as lacking the saccus, an internal extension of the vinculum. Male genitalia of *C. necyria* illustrate that the saccus is absent in some dioptids as well. The slender uncus and socii are hinged on the tegumen.

The aedeagus of *C. necyria* (Fig. 8) is typical in shape for members of Josiinae, being short, deep dorsoventrally, and large relative to the rest of the genitalia. A row of cornuti on the vesica, terminating in a set of robust, spinelike cornuti, is also common in the group (J. Miller unpubl.).



FIGS. 7, 8. Male genitalia of *C. necyria*. 7, Genitalia in posterior view with aedoeagus removed; 8, Aedoeagus in lateral view (anterior at left). At, anal tube; C, cornuti; Cs, costa of valve; D, diaphragma; E, opening of vesica; Sc, saccus; Sl, sacculus; U, uncus; T, tegumen; Th, ventral tooth of aedoeagus; Tr, transtilla; Vn, vinculum; Vs, vesica.

In female genitalia of *C. necyria* (Fig. 9), tergite 8 is membranous dorsally. The ostium is surrounded by postvaginal and antevaginal plates, which hinge on a point dorsal to the opening. There are small spines inside the proximal portion of the corpus bursae. A feature found in *C. necyria* and only a few other dioptids is the large, convoluted, sclerotized band which wraps around the corpus bursae. In noctuids, large muscles attach to the corpus (Callahan & Cascio 1963). Once the male has deposited the spermatophore in the corpus bursae, these mus-

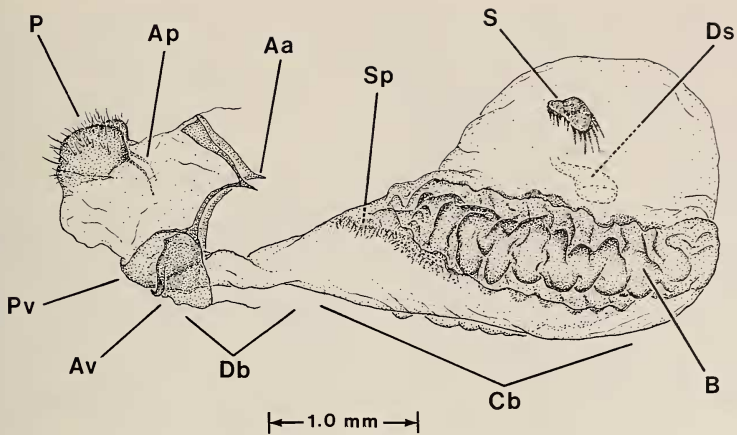
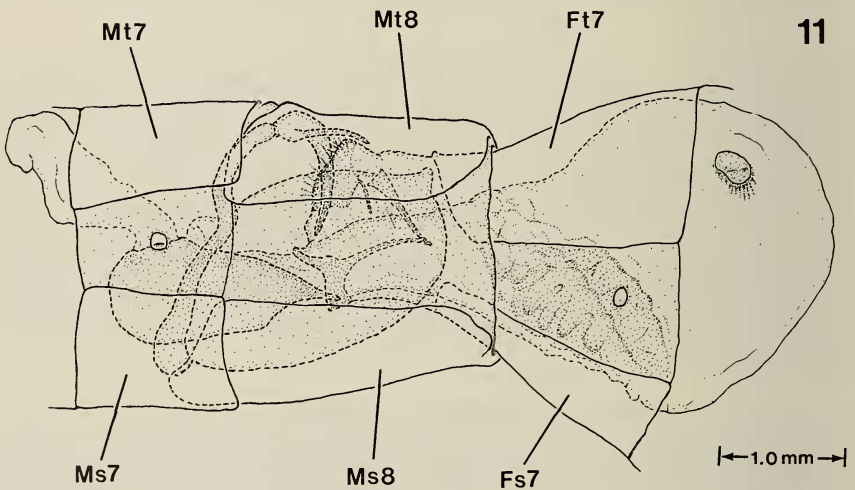
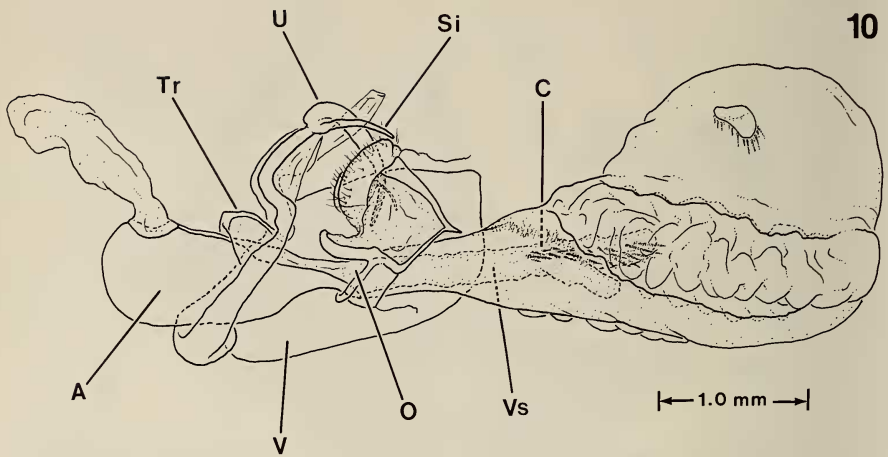


FIG. 9. Female genitalia of *C. necyria* in lateral view, anterior at right. Aa, anterior apophyses; Ap, posterior apophyses; Av, antevaginal plate; B, sclerotized band; Cb, corpus bursae; Db, ductus bursae; Ds, ductus seminalis; P, papillae anales; Pv, postvaginal plate; S, signum; Sp, basal spines of corpus bursae.

cles are thought to squeeze seminal fluid and sperm into the ductus seminalis. The sclerotized band of *C. necyria*, in conjunction with these muscles, may serve to break up the spermatophore. In *C. necyria* the ductus seminalis is located laterally on the corpus bursae, whereas in most diptids it is located on the ductus bursae (J. Miller unpubl.). The signum is composed of a group of long spines protruding into the corpus bursae from a concave sclerotized region. Petersen (1907) and Callahan (1958) suggested that the signum functions to hold the spermatophore in place. It is a site of muscle attachment in *Helicoverpa zea* (Callahan & Cascio 1963).

Copulatory Mechanism of *Cyanotricha necyria*

The interrelations of male and female genitalia during copulation are shown in Figs. 10 and 11. Between the papillae anales of the female, a membranous invagination allows for insertion of the male uncus, which is reflexed downward. In these preparations the uncus almost engages the postvaginal plate of the female. In freshly preserved material with the musculature intact, it most likely would do so. Stekolnikov (1965) found that the uncus engages the postvaginal plate in *Spilosoma menthastri*; the configuration he described is almost identical with that of *C. necyria*. Stekolnikov stated that the uncus in *Acronicta rumicis* engages the female's eighth sternite, but his illustration suggests that the 'eighth sternite' in *A. rumicis* is the same structure as the postvaginal plate in *Spilosoma* and *Cyanotricha*.



FIGS. 10, 11. Lateral view of male and female *C. necyria* in copulo, anterior of male at left, anterior of female at right. **10**, Pair #1 with abdominal segments 1-8 and left valve of male removed, and abdominal segments 1-7 of female removed; **11**, Pair #2 with abdominal segments 1-6 and left valve of male removed, and abdominal segments 1-6 of female removed. A, aedeagus; C, cornuti; Fs7, female sternite 7; Ft7, female tergite 7; Ms7, male sternite 7; Ms8, male sternite 8; Mt7, male tergite 7; Mt8, male tergite 8; O, ostium bursae of female; Si, socii; Tr, transtilla; U, uncus; V, valve; Vs, vesica.

In *C. necyria* the *socii* rest on top of the papillae anales during copulation and would seem to apply downward pressure on them (Figs. 10 & 11). A large muscle (“#1” in Forbes 1939) has its origin on the tegumen and its insertion at the base of the *socii*. This muscle has been observed in all Lepidoptera studied, and acts to flex the *socii* and uncus (Stekolnikov 1965, Arnold & Fischer 1977).

Judging from their position, the valvae of *C. necyria* apply lateral pressure on the female terminal segments. The sacculus is elongate and fairly rigid in most Lepidoptera. Muscles originate on the sacculus and insert on the clasper of the valve. When these are flexed, the claspers squeeze the female laterally (Forbes 1939, Arnold & Fischer 1977). The valve of *C. necyria* has a membranous sacculus and lacks a clasper (Fig. 7). It may be that only the valval costa provides traction during copulation.

Eversion of the vesica is effected by the combined forces of aerostatic pressure and muscle action (Callahan 1958). In Noctuidae the cornuti appear to serve two functions (Callahan 1958, Callahan & Chapin 1960): First, while the vesica is being everted, the cornuti, which at this time point inward, help drag the formed collum of the spermatophore into the ductus bursae. Secondly, when the vesica is fully everted and the cornuti point outward, they help manipulate the spermatophore so that it properly orients in the corpus bursae. Shape and orientation of the spermatophore is extremely specific in lepidopteran species (Williams 1940, 1941, Callahan 1960). Usually its aperture is placed in close proximity to the opening of the female's ductus seminalis. In addition, the movements of the vesica within the corpus bursae can be extremely complex. Callahan and Chapin (1960) argued that there is a “lock and key” mechanism at work during copulation that serves to inhibit mating between species. However, their research convinced them that it is not the relative shapes of the male valvae and female genitalia that is critical, as most previous authors had proposed, but is instead the configuration of the everted vesica and its ability to correctly place the spermatophore.

Unlike Noctuidae (Callahan & Chapin 1960, Takeuchi & Miyashita 1975) and Arctiidae (Stekolnikov 1965), the aedoeagus of *C. necyria* does not actually enter the female, but a small ventral tooth on the aedoeagus (Fig. 8) appears to insert into the antevaginal plate (Figs. 10 & 11). The diaphragma of *C. necyria* holds the aedoeagus tightly in place, whereas in many other Lepidoptera it is loose and allows the phallus to penetrate the female when the aedoeagus protractor muscles are activated (Forbes 1939, Stekolnikov 1965, Arnold & Fischer 1977). Opposing muscles insert on the saccus, and lack of movement of the aedoeagus in *C. necyria* may account for absence of the saccus. Judging

from the morphology of the diaphragma and aedoeagus in other dioptids, the characteristic of having only the vesica enter the female may define a restricted group of species. In copulating *C. necyria*, cornuti of the everted vesica were in apposition with basal spines of the corpus bursae (Figs. 10 & 11). This seemed to hold male and female genitalia together even after the left valve of the male had been removed. The two sets of spines may become entangled.

During copulation, the male genitalia of *C. necyria* are withdrawn into the abdomen to a point approximately even with segment 7 (Fig. 11). This is facilitated by the long intersegmental membrane between segment 8 and the ring (Fig. 4). It would be useful to know which muscles pull the genitalia in. Their morphology may prove to be another unique feature of dioptids and notodontids. In *C. necyria* the tergite and sternite of male segment 8 have an important holding function; when the female is pulled into the male abdomen, they appear to apply dorsoventral pressure on her seventh segment. Highly modified male eighth tergites and sternites are found in many notodontid and dioptid species (Franclemont 1970, Holloway 1983), which suggests that a holding function is typical for the group, and possibly represents a synapomorphy for the entire lineage.

CONCLUSIONS

One feature of copulation seems common to all lepidopterans studied: the male uncus is inserted between the papillae anales and applies pressure on the dorsal surface of the female's postvaginal plate. Other aspects are unique to each species. The female of *Speyeria* is held at three points: the uncus secures the tergum of segment 8, valvae apply lateral pressure on the papillae anales, and the base of the valve secures sternite 7 of the female (Arnold & Fischer 1977). In *Carcharodus* the intersegmental membrane between segments 7 and 8 of the female is expanded. The uncus engages the postvaginal plate, and valvae grip the female's intersegmental membrane (De Jong 1978). There are two points of contact in *Spilosoma* and *Acronicta*: the uncus secures the female postvaginal plate, and valvae apply lateral pressure at the base of the ductus bursae (Stekolnikov 1965). My study has shown that the female of *Cyanotricha necyria* is held in three places: the uncus engages the female postvaginal plate, valvae grasp her terminal segments laterally, and the male eighth abdominal segment applies dorsoventral pressure on female segment 7. A fourth possible point is the cornuti of the vesica, which seem to become entangled with spines located at the base of the corpus bursae, but dissection of freshly preserved material is required to confirm this.

Copulation in *C. necyria* is unique among Lepidoptera so far de-

scribed in that an exceptionally long membrane between abdominal segments 8 and 9 of the male allows the female to be pulled into the abdomen during copulation. The male eighth segment then aids in grasping the female, and may provide the majority of force for holding the pair together. This trait could prove to be another synapomorphy for the dioptid-notodontid lineage, but its distribution among species has not been adequately documented. Such information may be crucial in clarifying phylogenetic relations among these taxa.

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